A SKETCH OF COMPARATIVE EMBRYOLOGY.

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V.—THE GENERAL PRINCIPLES OF DEVELOPMENT.

THE sponges present, as we have seen, many exceptional peculiarities in their development. All the remaining Metazoa, on the other hand, may be treated as members of one series, which are governed by several general laws of embryonic growth, only a portion of which can, at present, be said to apply to the sponges.

The fundamental law of embryology is, that the simple precedes the complex, the general and typical, the special. All embryos obey this principle in their early growth, and most of them throughout all their growth; but some, after advancing to a certain stage, stop, or suffer a degeneration as it is technically called—in other words, only a part of their organs continue to develop; or even the whole animal retrogrades, *i. e.*, becomes simpler. Of degeneration,[1] the Crustacea offer many instances—one of the most familiar is the common barnacle, which in its young or larval state swims about the ocean freely, having well developed limbs and sense organs, but later loses some of its structures, becoming in its adult condition permanently attached to the rock. Almost all parasitic forms are degraded. In spite of these instances, progress is primary and universal, degeneration secondary and exceptional. In all cases the embryos present to us animals stripped of the secondary modifications found in adult life, and exhibiting the more essential peculiarities. Thus in very young birds we plainly recognize the gill slits and arches corresponding to the gills of fishes, but in the adult bird the gill slits have disappeared, and the arches so metamorphosed, that without knowing the embryo it would hardly be possible to discover their real connections, and their identity with the corresponding structures of fish. Embryology has proved that gills are typical of vertebrates, although many vertebrates have none in the adult state. Such insight the student of embryology may gather from any animal and every organ.

The next law is, that development is always gradual—to it there are no exceptions. Even the sudden metamorphoses, *e. g.*,

[1] E. Ray Lankester has recently published a very interesting little volume on degeneration in the Nature Series.

of caterpillars, are only apparent not real exceptions, for in the caterpillar the chrysalis is gradually formed, and when perfected is merely uncovered by the casting off of the caterpillar skin, which masked the changes going on within, and so also the opaque crust of the chrysalis conceals the butterfly being formed underneath. In some animals, however, the *visible* changes though still gradual are more rapid at one time than another, as when the larval starfish (Brachiolaria) passes in a few hours into the adult form. The explanation of the gradualness of development in the Metazoa, is the dependence of the process on alterations in the single cells, and as these are small and change slowly, the whole effect is produced imperceptibly; we notice only that the embryo has advanced since we examined it before, we cannot see it advancing.

Now, the construction of an animal out of the cells derived from the impregnated egg, depends on two things; *first,* the arrangement of the cells in relation to each other; *second,* alterations in the characters of the cells themselves. We have already seen that in the course of segmentation the cells become arranged in two layers, the *ectoderm* and *entoderm,* both consisting of a single stratum of cells, and later there is a set of cells, the *mesoderm,* in between, Fig. 20. Compare also Fig. 15, p. 248.

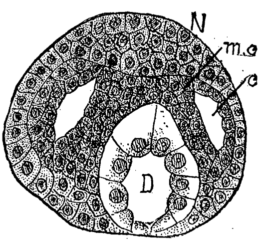

FIG. 20.—Transverse section through the head of embryo *Lumbricus trapezoides.* After Kleinenberg.

Before proceeding further it is desirable to say a few words about the middle germinal layer. Concerning its origin we have but little satisfactory information. In the lower animals (Radiates) it arises from cells which break away from the two primitive layers. In the jelly fishes it hardly exists as a distinct part, but as the Brothers Hertwig have shown, is rather an incompletely separated portion of the ectoderm. In the Bilateralia, or all animals except sponges and radiates, the mesoderm is always present as a distinct layer, which is formed *after* both the ectoderm and entoderm. Its exact origin has never been definitely settled, although the question has been interminably discussed, especially as regards vertebrates. It is, however, known that in some forms there are two special cells, one at each side of the primitive mouth of the gastrula, distinguished by their large size and containing a

large amount of nutritive matter. These cells are called the *mesoblasts*, and break up into smaller cells which form the middle germinal layer, Fig. 21. The cut represents a longitudinal section through the *double* embryo of *Lumbricus trapezoides*, after Kleinenberg. In this species the development is unique, for each egg normally grows into two individuals. The separation begins during segmentation. The two embryos are united by a cord of large cells, Fig. 21 *u*, and have at first a common mouth. In the right hand embryo of the figure, the large mesoblast lies between the inner and outer layers, and has already given rise to a number of cells, *mes*, the beginning of the mesoderm. In other cases it has been said that the mesoderm arises from the ectoderm or the entoderm, but nearly every observer is contradicted by some other, therefore it would be unprofitable for us to pursue the matter further. Suffice it to say that the embryonic mesoderm of the Bilateralia consists of a *mass* of cells, or of *several strata* when the mass is compact, whereas the other two layers are each but one cell thick. This difference is always preserved, except in the ectoderm of vertebrates, to which we shall recur. This is our third law.

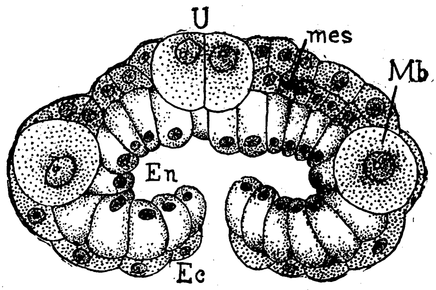

FIG. 21.—Double embryo of *Lumbricus trapezoides*, longitudinal section. After Kleinenberg.

The fourth law is that the cells are grouped in definite relations to certain ideal axes or planes. The first of these axes is the *gastrula* or *dorso-ventral;* it alone is clearly indicated in the Cœlenterata. It is the line which passes through the mouth of the gastrula and the opposite end of the body, Fig. 22 *A*.

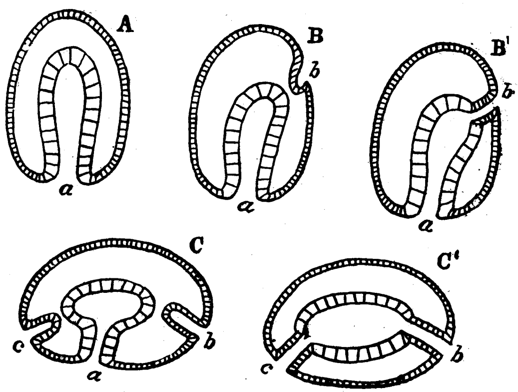

FIG. 22.—Diagrams to show the axes of the body: *A*, with mid gut alone; *B*, with fore gut: *C*, with fore gut and hind gut; *a*, opening of gastrula; *b*, of fore gut; *c*, of hind gut.

In order to understand the relation of the other axes, we must consider briefly the development of the digestive canal in the Echinoderms, and some bilateral animals. The diagrams in Fig. 22 show the points which concern us now. The ectoderm in the young Echinoderm gastrula forms a little pit, Fig. 22 *B*, *b*, near the upper end of the gastrula stomach; the bottom of this pit grows onto the wall of the stomach, an opening breaks through and the pit and the stomach form a continuous canal with two orifices, Fig. 22 *B'*. A plane passed through these two openings and through the gastrula axis will divide the body into symmetrical halves, a right and left. This plane may be called the median plane. It is of course purely ideal, not present as a structure of the embryo. In the young mollusk, a snail for instance, beside the first ectodermal pit, Fig. 22 *C*, *b*, there is formed a second one, and always in such a position that the median plane passes through it, while the gastrula mouth lies between the two involutions of the ectoderm. The gastrula mouth ultimately closes, the two pits become connected with the entodermal cavity, their exterior openings forming respectively the mouth and the anus. A line passed through these two secondary openings represents the longitudinal or antero-posterior axis. It must not be imagined that these axes necessarily always remain straight, for, on the contrary, they usually depart somewhat from the simple form, sometimes very much so, as in the case of the spirally twisted snails. These axes mark the distinction of dorsal and ventral surface, of right and left sides, of anterior and posterior ends or head and tail. In the vertebrates the axes are further complicated in a manner which will be studied in a special article, and is therefore passed over here.

The fifth law is that, however much the weight of an animal increases during its development, the ratio of the free surfaces to the mass alter but slightly from the ratio established when the embryo begins to take food from outside. It is only for convenience that I express this law in this precise form—in reality, about it our knowledge is scanty and our conceptions vague. According to a geometrical principle, when the bulk of a body bounded by a simple surface increases, the surface enlarges less than the mass —in the simplest case of a cube, the surface increases as the square, the mass as the cube of the diameter. If in a cube of unit diameter, one unit of surface bounds one unit of mass, then

in a cube of three units diameter, *nine* units of surface will bound *twenty-seven* units of mass; the proportion in the first cube is 1 : 1, in the second 1 : 3. To maintain the proper proportion in the embryo, simple enlargement is insufficient, therefore the surface becomes more and more irregular or uneven, being thereby multiplied to correspond with the bulk. The irregularities present distinctive peculiarities characteristic of each organ and part, and may be either large or microscopic. They may be conveniently classified under five heads: 1. Projections, either large like the limbs of insects and quadrupeds, the tentacles of Cœlenterates, the branchia of Amphibia, etc., or microscopic like the *villi* of the intestine.[1] 2. *Dilatations* of the digestive canal and other internal cavities; the stomach is usually a dilation. 3. *Diverticula*, or blind pouches, pushing out from one part or another; the lungs of vertebrates, for example, are diverticula of the digestive tract. 4. *Folds*, or ridges either longitudinal or transverse. A capital illustration is afforded by the common grasshopper (Caloptenus); this insect has six large diverticula springing from the front end of its stomach, each of which is traversed by twelve longitudinal folds, admirably shown in transverse sections, Fig. 23. 4. Small pits, or *invaginations*, which form glands. They differ from diverticula by their smaller size, and also in that they grow *into* the mesoderm, while the diverticula push the mesoderm along with them. A section through a couple of such pits is shown in Fig. 24, which represents "mucous glands" from the stomach of a kangaroo. It will be noticed that the cells at the bottom of the pit are larger than those nearer its mouth, so that the lower *glandular portion* is already marked off from the upper part or *duct*. Of *pits*, or *glands* as they are prop-

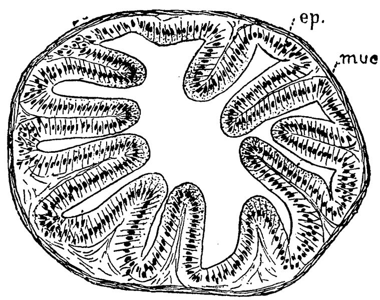

FIG. 23.—Transverse section of gastric cœcum of *Caloptenus spretus; ep*, entodermal epithelium; *muc*, muscles; *conn*, connective tissue. × about 40 diam.

[1] To see the *villi*, of which students usually have a very imperfect conception, it is only necessary to take a short piece of small intestine of a common mammal (dog or rat), slit it lengthwise, spread it out, wash it and examine with a lens. Although the inner surface of the intestine would be very small if it were smooth, yet in reality it is very great, being increased by the countless villi and glands.

erly called, there are many kinds, varying in shape and in the character of the cells lining them. They may be straight or very much elongated and coiled or twisted; they branch in many different ways, but all forms are modifications derived from simple pit-like invaginations.

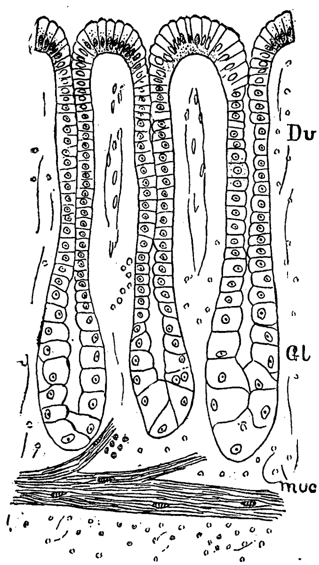

FIG. 24. — Vertical section of mucous glands from the stomach of *Macropus giganteus*. After Schaefer. × 210 diam.

The necessity of proportioning the surface to the mass arises from the fact that it is only through the surface that food, water and oxygen can be taken in, refuse matters (excretions) ejected, and sensations from the outside received. Hence when the right relation is once established it must be permanently kept up. In the growing embryo the object is so to expand the surface that as the bulk increases, the surface is always sufficient not only to supply the cells composing it, but also the inner and deeper lying tissues.

We can now understand why eggs with very little yolk are hatched very early, to become self-dependent larvæ—it is because of their small bulk, which enables a simple surface to answer their physiological needs, to digest and breathe enough. Bulkier eggs must reach a more advanced development, living the while on their own yolk, before they can lead a free life. Let it not be thought, however, that any one has ever determined, even in a single case, the proportion between the surface and the mass. There are reasons for thinking that the proportion varies considerably in different species, and even in individuals of the same species.

The sixth law is, that in all but the lowest metazoa, there are several systems of cavities formed in the mesoderm. The mesoderm becomes more important and voluminous as we ascend the animal series, and so also do the cavities of the middle layer become more complex. In many animals there is one large space known as the body cavity, but the other spaces are for the most part small; such are the organs of the circulation, the blood ves-

sels, and in vertebrates the lymphatic system. Another set of cavities forms the excretory system—the water vessels (of certain worms), the segmental organs and kidneys, all distinguished by being connected directly with the exterior by openings through the ectoderm. There are also tubular ducts which compose the secondary genital apparatus, and are, in many of the higher invertebrates and in all vertebrates, intimately connected with the excretory organs. Formerly it was supposed that the branching respiratory tubes or *tracheæ* of insects, were mesodermic, but more recent investigations tend to show that they are always invaginations of the ectoderm. All these cavities are lined each by a layer of cells, one row deep, an *epithelium*. In the circulatory channels and body-cavity, the epithelium appears to be invariably composed of broad, irregularly polygonal very thin cells, being a so-called pavement epithelium, while in the excretory tubes and genital ducts the epithelium is quite thick, each cell being at least as high as it is broad.[1]

The seventh law is of the utmost importance—each germinal layer forms predetermined special tissues, and no others, and each tissue in a predetermined position. In all bilateral animals at least, the mesoderm forms, besides the organs belonging to it exclusively, such as the heart, etc., layers of tissue around the whole entoderm and ectoderm; for example, the intestine of an adult animal is composed of an entodermal lining (epithelium) and several mesodermic coats (connective tissue and muscles); the skin is composed of an outside *epidermis*,[2] derived from the ectoderm, and under it the *dermis*, or cutis, derived from the mesoderm. An organ is said to be ectodermal or entodermal when the part essential to its physiological function arises from one or the other of the primitive layers; for example, the eye is ectodermal because its light perceiving portion is developed from the outer germ layer; the liver on the other hand is entodermal because its secreting cells are formed from the inner germ layer.

The anatomy of adult forms does not by any means always reveal to which layer a given organ properly belongs. This is perhaps better illustrated by the nervous system than by any

[1] There are certain exceptions, *e. g.*, the malpighian bodies of the vertebrate kidneys are lined by a pavement epithelium although they form part of the excretory system of cavities.

[2] Often called *hypodermis* by many writers on Invertebrates, especially by entomologists.

other structure. In nearly all animals the central nervous system (nerve ganglia, spinal cord, etc.) lies quite deep, well separated from the ectoderm or skin, yet in the embryo the nervous system arises from the ectoderm (Fig. 25, *cf.* also Fig. 20) appearing at first as cells very much like the rest of the ectoderm. They soon, however, separate from their first neighbors, moving inwards; the mesoderm then grows in between the half developed nervous cells and the ectoderm, so that they are completely divided.

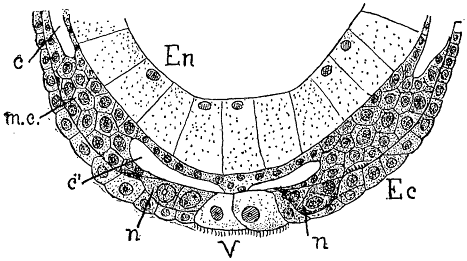

FIG. 25—Transverse section of embryo *Lumbricus trapezoides*. After Kleinenberg. *En*, entoderm; *Ec*, ectoderm; *n*, *n*, beginning of nervous system; *v*, ciliated band separating the two parts of the nervous system; *c*, *c'*, parts of body cavity; *m.c.*, mesoderm. Only the ventral half of the section is figured.

The following table shows to which of the germ layers the principal organs belong:

ECTODERM.

1. Epidermis or external skin.
   The crust of arthropods.
   Shell of mollusks.
   Horns, hairs and nails.
   Cutaneous glands.
   Cilia of larva, etc.
2. Nervous system.
   Organs of, *a* Touch.
   b Taste.
   c Smell.
   d Hearing.
   e Sight, etc.
4. Fore gut.
5. Hind gut.
6. Mouth gut (vertebrates).
7. Gills.
8. Tracheæ of insects.

MESODERM.

1. Wandering cells.
2. Connective tissue, fat cells, etc.
3. Internal skeleton.
4. Muscles.
5. Genital products.
6. Blood.
7. Organs of circulation.
8. Organs of excretion.
9. Secondary genital organs.
10. Lymphatics (and spleen).

ENTODERM.

1. Middle gut.
2. Liver.
3. Lungs.
4. Glands.
   Thyroid, pancreas, etc.
5. Various appendages of the digestive canal.

As appears from this table the destiny of each germ layer is predetermined.

The eighth law is, that the simple cells formed during segmentation change their character during embryonic growth, not only appearing differently but altering also their activity from general

to special functions. Of course it is not possible to consider here in detail the laws of histological differentiation, the more as they have never received much attention, for although hundreds of published researches elaborately describe the changes in special cases, yet the general laws of the progressive development of cells have never been seriously discussed, and rarely subject to more than incidental treatment. I shall mention only three general principles, which are at once universally applicable and readily understood. 1. Structural modifications of epitheliums usually affect similarly a whole cluster of cells; or 2. Less frequently isolated cells only. 3. The mesodermic tissues are for the most part in masses (muscles, tendons, fat, etc.) not in layers, excepting always the epithelial lining of the mesodermic cavities.

We have already considered one illustration of the first principle, the formation of the central nervous system (Fig. 25, *n*, *n*). Other areas are transformed into the retinæ, the finger nails, etc. Again smaller clusters into the lining of glands. Let us consider for a moment the peptic glands of the mammalian stomach, which are modifications of the simpler mucous glands (Fig. 24). The peptic gland is still a straight tubular pit running down from the inner surface of the stomach, but the cells composing its walls are of several kinds—one sort in the neck, *a*, two in the glandular portions, *b* and *c*, of which the darker and more closely granulate cells ("*Belegzellen*") predominate in *b*, but the lighter central cells, *h* ("*Hauptzellen*"), in *c*. The central cavity of the gland is not shown in *b* and *c*. The relative positions of the two kinds of cells will perhaps be better understood by a transverse section, Fig. 27, through the lower part, Fig. 26 *c*, of a cluster of glands, such a section being of course parallel to the inner surface of the stomach. We here have an excellent illustration of what is meant by histological differentiation, for the general arrangement of the cells is the same as in Fig. 24, but in different parts of the more complex peptic gland they have assumed distinct forms and functions.

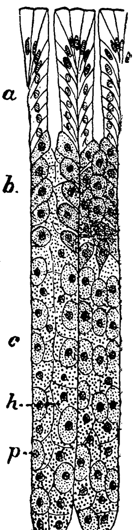

FIG. 26.—Peptic glands from stomach of guinea pig; *a*, neck; *b*, middle portion; *c*, basal glandular parts; *h*, "hauptzellen;" *p*, peripheral cells. After Rollet. × 160 diam.

The differentiation of isolated cells is often very important. In

the skin of many animals there are unicellular glands. Every minute scale making the microscopic dust on a butterfly's wing results from the modification of a single cell, from which the scale grows out; again in the ectoderm of Cœlenterates, Fig. 28, we usually find scattered among the unmodified epidermal cells single nettle cells (thread or lasso cells), *l*, and unicellular glands. The nettle cells may be readily recognized by the coiled thread in each of them; the gland cells by a small pore and their mass of secretion, Fig. 28 *D*.

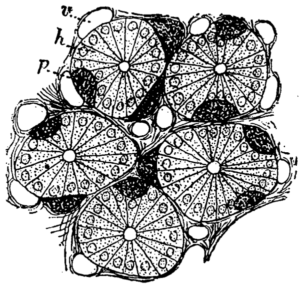

FIG. 27.—Transverse section across five peptic glands of a domestic pig; *v*, blood vessel; *h*, "hauptzellen;" *p*, peripheral cells. After Rollet. × 320 diam.

Such are the leading principles of embryology as far as our space permits dealing with them, varying however in their exact application from group to group. In all the embryos of each natural group, we can recognize peculiarities common to all the members of the group, peculiarities which we therefore designate as typical. When, however, the embryonic form leads a free life, it may often present special adaptations that change it so much as to obscure the typical features, hence in the study of those forms which begin their free life in an embryonic condition, we have to compare the larvæ, one with another, in order, by the elimination of those features which are only special and secondary, to discover the really typical structure. This is particularly the case with marine animals, whose larvæ often have bizarre shapes, which have arisen, it is to be assumed, by natural selection among the larvæ, and relate to their presentation rather than directly to their development. Therefore we shall not pause to consider the forms of embryonic larvæ. I hope, however, to publish, before long, figures which will enable the student to recognize the more common marine embryos.

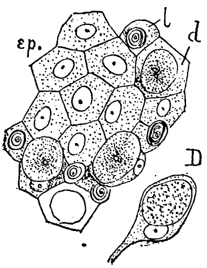

FIG. 28.—Ectoderm of Tetrapteron; *ep*, modified epidermis; *l*, lasso or nettle cell; *d*, gland cell. *D*, side view of gland cell. After Claus.